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An Analysis of Sauger Maturity Regimes in Southern Lake Winnipeg.

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An analysis of sauger maturity regimes in southern Lake Winnipeg.

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ABSTRACT

Visual and histological determinations of sex and maturity of walleyes and saugers from the south basin of Lake Winnipeg are compared. Visual determinations of sex, irrespective of maturity, are accurate. Visual maturity discrepancies are largest in summer and smallest in spring. An evaluation of visual discrepancies in autumn is confounded by the inability to distinguish between a new spawner (immature) and a former spawner (mature), since both exhibit gonadal development.

Visual maturity determinations tend to overestimate proportions of immature individuals in spring and summer and of mature females in autumn.

Maturity in female saugers is size-specific.

Age-specific and size-specific seasonal maturation rates of female saugers based on visual determinations are generally less than those based on histological determinations.

The greatest difference between visual and histological maturation rates occurs in autumn.

The mean weighted ages of onset of sexual maturity of female saugers (Abrosov 1967) are greater than the mean ages of maturity derived from fitted maturity curves irrespective of season or type of maturity determination. The greatest difference between values obtained by these two methods (1.88 years) occurs in the fall visual category. The best estimate of the mean age at maturity of female saugers is 5.08 years.

The best estimate of the mean size at maturity of female saugers is 303.36 mm.

Visual determination of maturity of female saugers in autumn produces non-significant age-specific and size-specific maturity curves because developing fish are classified as being mature.

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INTRODUCTION

This study was initiated in the spring of 1976 to investigate the maturity status of walleye (*Stizostedion vitreum*) and sauger *(Stizostedion canadense)* in the South Basin of Lake Winnipeg. The project was designed to examine seasonal variations in gonad development and the size and age of fish at maturity. Sampling was confined to the open water seasons.

Valid sex and maturity data are necessary for the evaluation of the following reproductive parameters:

1. The maturation rates of the sexes.
2. The mean age or size at maturity (the mean age or size at which 50% of each sex is mature).
3. The growth rates of the sexes.
4. An estimate of whether or not a fishery is exploiting a population before the stock has had a sufficient chance to spawn.

Of primary concern to this study is the reliability of sex and maturity data which depends on the ability of workers to correctly classify sex and maturity, especially in the field, and on the time of year that populations are sampled. Deason (1933) sampled walleyes in late spring and early fall but found sex differentiation difficult in immature individuals. Carlander (1945) indicated that sexing walleyes was difficult during summer months. Kennedy (1949) experienced

difficulty in sexing immature walleyes in winter. Wolfert (1969), Priegel (1969) and Payne (1964) sampled walleyes during early spring, late fall and winter, respectively, in order to assess maturity. There is no documented study that accounts for seasonal variations in the reliability of sex and maturity determinations.

The specific objectives of this study are:

1. To review the literature on the maturation cycles in walleye and sauger.
2. To compile a "sex and maturity manual" to aid field workers in classifying sex and maturity during the ice-free seasons.
3. To determine the amount of discrepancies in visual classifications of sex and maturity.
4. To determine at what time of year the populations of walleye and sauger should be sampled in order to realistically depict maturation schedules.
5. To determine whether maturation of walleye and sauger is age-specific or size-specific.
6. To determine whether or not the "developing" category is valid or useful and to reinforce the "immature" and "mature" categories.

LITERATURE REVIEW

The nature of oogenesis and spermatogenesis (maturation) governs the nature of spawning and is of prime importance in a study of reproductive dynamics.

Ball (1960) describes oogenesis and Hoar (1969) describes oogenesis and spermatogenesis in a generalized teleost: in the ovary, oocytes and follicle (granulosa) cells arise from specialized epithelial cells (the germinal epithelium) which penetrate the lumen in a series of ovigerous folds. The ovarian stroma is highly vascularized and is rich in elastic tissue and smooth muscle. Each oocyte becomes surrounded by a single layer of granulosa cells to form the ovarian follicle which eventually develops into the mature ovum. Growth occurs in two phases. The first phase is slow and cytoplasmic; the second phase is rapid and involves the deposition of large amounts of yolk. In the testis, the germinal epithelium is not permanent. Nests of spermatogonia (cysts) proliferate from resting germ cells and migrate along a series of seminiferous tubules which penetrate the organ ventrally and laterally. Maturation within each cyst is synchronous in that all the cells are at, or nearly at, the same stage of development. When spermatogenesis is complete the seminiferous tubules are packed with spermatozoa.

Percids, like all other temperate zone fishes, have an annual reproductive cycle which corresponds to regular seasons

of temperature and day length (Hokanson 1977). This seasonal cycle ensures optimal hatching and growing conditions for succeeding generations. Reproduction in tropical species is not as seasonally defined. Maturation and spawning occur simultaneously throughout the year (Ball 1960).

Naumov (1956) and Ball (1960) mention two types of spawning in seasonally breeding fishes: isochronal or total spawning and batch or partial spawning. In isochronal spawners oocyte growth is synchronous in that once a year oocytes develop simultaneously to maturity. Eggs are spawned in one batch or in portions over a few hours or days. Batch spawners have asynchronous oocyte growth in that several portions of oocytes develop to reach maturity at different times. Spawning takes place in distinct batches over an extended period. A more definitive maturity staging is made possible for species with isochronal spawning since at any one time the majority of oocytes are in the same developmental phase (Bagenal and Braum 1968). Perca sp. and Stizostedion sp. exhibit synchronous oocyte growth which is most pronounced in Eurasian perch, yellow perch, and walleye (Hokanson 1977). Koshelev (1963) found that oocyte growth in pike-perch was more asynchronous than in perch and that batch spawning occurred in certain reservoirs.

Various authors propose maturity classification schemes based on gross inspection of gonads for species with isochronal spawning. Kesteven (1960) and Nikolsky (1963) give generalized classifications. James (1946) and Naumov (1956) report on

largemouth bass and Murmansk herring, respectively. These elaborate schemes involve from six to nine categories. They rely on subjective criteria such as size, shape, color, degree of vascularization, size and color of eggs, etc. Classification schemes for walleye or sauger are lacking although Eschmeyer (1950) discusses the identification of sex and the development of the reproductive organs in walleye.

Maturation cycles based on histological examination of gonads in Percids are described by Koshelev (1963), Golovanenko et al. (1970), and Turner (1919). Standard histological techniques involving fixation in Bouins or Zenkers fluids, embedding in paraffin, sectioning, and staining with hematoxylin and eosin etc. are used. Criteria such as cell-size, staining quality, follicular membrane structure, degree of vacuolation, and degree of fat and yolk deposition are used to determine stages of maturity.

Koshelev (1963) describes stages of maturity in Eurasian perch ovaries based on phases of oocyte growth: the transitional post-spawning stage (VI-II) generally lasts from mid-May to mid-June and is characterized by resorption of remnants from the emptied follicles. Stage II follows only upon completion of resorptive processes and generally lasts until late August. It is a period of low oocyte growth and is divided into three substages: relative rest (IIA), active oogenesis (IIB), and initial vacuolation (IIC). Substage IIA is characterized by a large number of oocytes in the monolayer follicle phase (low growth phase) and a small number of oogonia and primary oocytes. Primary oocytes, oogonia, and

later phases of oocyte growth increase in number during substage IIB. During substage IIC a portion of oocytes in the low growth phase begin to show vacuolation. The duration of stage II in repeat spawners is eight times shorter than in first-time spawners.

Stage III begins with the seasonal reduction in water temperature and lasts until late October. It is a period of active growth, and is characterized by oocytes in the late phases of vacuolation and the initial phases of yolk formation.

Stage IV is the period of major oocyte growth and lasts from early November through May. It is divided into two substages: IVA and IVB. In substage IVA an intensive accumulation of yolk and fat begins. By the end of winter ovaries are in substage IVB which is characterized by an increase in yolk grains and a fusion of small fat droplets into larger ones.

Stage V (ovulation and spawning) occurs on the spawning grounds and only lasts a few days. In perch, it is divided into two substages as the roe is spawned in characteristic egg-bearing ribbons. For the majority of fish species,stage V occurs when yolk merges into a homogeneous mass and single fish eggs are released from follicles.

Golovanenko et al. (1970) use the method of Trusov (1949) to determine maturity stages in pike-perch. His stages of maturity and those of Koshelev (1963) differ somewhat in their durations but are similar in their descriptive characteristics.

Both describe two distinct periods of oocyte growth: a period of lesser growth which lasts from spawning through late August, and a period of major growth which begins with a seasonal reduction in water temperature and lasts through to spawning.

Golovanenko et al. (1970) also document the physiological and biochemical changes occurring in the ovaries, blood, and liver throughout the maturation cycle. During the post-spawning stage and the period of low oocyte growth, free amino acids and protein in the ovaries are at a minimum. Due to intensive post-spawning feeding a maximum quantity of fat accumulates in the liver and viscera and levels of lipid, protein, and hemoglobin in the blood are high. Protein reserves accumulate in the liver. During the phases of major or trophoplasmic oocyte growth, fat and protein reserves are depleted. Gonadal fat and protein increase steadily and attain high levels which remain stable during winter. During the spawning migration, levels of serum protein, lipid, and hemoglobin are reduced. Oocyte protein increases sharply at the expense of food protein. On the spawning grounds, protein and lipids in the blood and liver are at minimum levels. The level of blood-hemoglobin is inversely proportional to the coefficient of maturity.

Turner (1919) describes the stages of maturation in the spermary of the yellow perch as follows: the resting stage and period of germ cell migration occurs shortly before spawning and continuously until early September. It is characterized by the active migration of germ cells to the peripheral lobules

of the testes. The period of proliferation and growth begins once the first germ cells have become lodged. This period lasts well into November. The first germ cells attain maximum size in early August at which time spermatogenesis begins. During the transformation into spermatozoa there is a general reduction in cell-size accompanied by a tendency for the cells to stain more darkly. The first spermatozoa are formed in early September and are present until spawning. Expulsion is not complete and a few spermatozoa can still be found during early summer months. Spermatogenesis and an increase in testicular volume begins with the seasonal reduction in water temperature.

The seasonal cycle in gonad size is widely used to investigate maturation cycles. The maturity or gonadosomatic index (% gonad weight/body weight) is used by LeCren (1951) to trace the seasonal cycle in gonad weight and condition in the Eurasian perch. Similar results are obtained by Turner (1919) for male yellow perch, Brazo et al. (1975) for female yellow perch, and Eschmeyer (1950) for walleye. Payne (1964) traces the cycle in gonad volume in walleye.

LeCren (1951) finds that the maturity index (MI) is constant at any one season for all sizes of fish of the same sex and stage of maturity. In ripe individuals the MI averages about 20% for females and 8% for males. Freshly spent ovaries average about 3% of the body weight and by mid-June have reached 1%. They remain at this ratio until August. Through April and May the MI in males decreases to 1 - 2% and

remains at this level through June, July,and most of August. The MI for both sexes begins to increase in August, though somewhat earlier in females. By October the testes have reached maximum size whereas the MI for females continues to increase regularly until spawning. In immature males and females the MI remains constant at about 0.5% throughout the year.

The occurrence of resorptive processes in female percids can provide evidence of maturity and can affect the cyclic nature of spawning. Based on visual examination, unspawned ova (residual eggs) are numerous in walleye ovaries in early spring and average about 2.8% of the total eggs. Smaller proportions can still be found in at least some specimens from late August (Eschmeyer 1950). Koshelev (1963) distinguishes between first-time and repeat spawners throughout the year by microscopically examining ovarian tissue for the remnants from the structureless membrane (zona pellucida) of the emptied follicles. Koshelev (1963) and Brazo et al. (1975) rarely find residual eggs in perch based on gross inspection of ovaries. Since perch eggs are spawned in an egg-bearing matrix and walleye or sauger eggs are broadcast singly, residual eggs are much less likely to occur in perch. According to Koshelev (1963) oocyte growth begins only upon completion of resorptive processes. Poor growth conditions can reduce the rate of these processes and delay the period of oocyte growth causing the next spawning period to be missed (Hokanson 1977). Golovanenko et al. (1970) find that a protracted spring causes more synchrony of maturation in

pike-perch. Interrupted spawning due to the onset of cold weather can cause resorption of ova in walleye (Derback 1947). During fall months the proportion of "non-ripening" female walleyes (with ovaries typical of spent fish) can be as high as 16% in years of poor growth, but usually is less than 5% (Forney 1965).

MATERIALS AND METHODS

Walleye and sauger were collected from the South Basin of Lake Winnipeg in May and July 1976, September 1977, and from June 1 to October 5, 1979. Gill nets were used exclusively. Mesh sizes ranged from 7.62 cm to 10.80 cm. During spring and summer commercial fishermen were hired to capture fish or they were purchased from commercial fish plants. In fall months fish were obtained from experimental netting operations.

Specimens were examined in fresh condition or were frozen as soon as possible after collection. Fork lengths were measured to the nearest 2 mm and round weights to the nearest 20 g. Scales, from above and below the lateral line, otoliths, dorsal spines, and pectoral fin rays were taken from each fish for aging studies. The sex and state of maturity of each fish was determined visually. Color photographs were taken of most gonads *in situ*. All gonads were labelled and stored in 10% formalin for histological examination.

Each fish was classified as being immature, developing or mature. Three "uncertain" categories were used for histological classifications, as specimens sometimes showed characteristics common to more than one category. According to definitions given by Balon (1975) and Payne (1964) a fish is considered mature if it is ripe or has spawned. Since ripe specimens were not sampled, a fish was considered as mature only if it showed evidence of having spawned.

A fish was considered as immature if gonads showed no evidence of former spawning or, during fall months, if they showed lack of development towards subsequent spawning. The developing category was used in an attempt to distinguish between new spawners and former spawners. A developing individual lacked evidence of former spawning but did show gonadal development.

Visual sex and maturity was determined by gross inspection of gonads in situ. Criteria (Table 1) were adapted from Eschmeyer (1950), Kesteven (1960), and Nikolsky (1963).

Histological sex and maturity was determined by macroscopic and microscopic inspection of preserved gonads. All gonads were dissected and examined under a stereoscopic microscope at 4X - 60X and were classified according to criteria listed in Table 2.

Sex was determined histologically by staining gonadal tissue with aceto-carmine. The technique was identical to that described by Guerrero and Shelton (1974) except that it did not work equally well on fresh specimens and gonads were not stored in alcohol. Ovarian tissue was positively identified by the presence of oocytes. Spermatogonia could not be distinguished.

The technique was also used to examine ovarian tissue in an attempt to accurately determine phases of oocyte growth. Only two basic types of oocytes could

Table 1. Visual criteria for classifying sex and maturity in walleye and sauger.

Maturity Category	Sex	
	Female	Male
Mature	- flaccid, sac-like appearance	-reduced in size, flaccid appearance, sharply tapered.
	- residual eggs scattered irregularly about the ovary. Appear as small, round, yellowish-white spots	-greyish-white coloration
	- bluish-red coloration	-smooth, glossy, soft in texture
	- transverse blood vessels	-dorsal blood vessel in shallow groove
	- dorsal blood vessel on surface	
Immature	- transparent with scattered pigment usually in narrow band along each side of mesovarium	-transparent with little or no pigment on fine, thread-like testes, much smaller in cross section than ovaries
	- ovaries cylindrical with transverse blood vessels which become more conspicuous with increasing size	-lacks transverse blood vessels
	- anterior tips broadly rounded or come to a blunt end	-anterior tips tapered rather than blunt or rounded
	- often much less than length of swim bladder	-usually same length as swim bladder
Developing	- ovaries enlarged. Occupy ½ to 2/3 of ventral cavity	-testes enlarged. Occupy ½ to 2/3 of ventral cavity
	- reddish to orange coloration	-reddish to white coloration
	- eggs clearly discernable	-with increasing maturity testes appear milk-white, smooth, glossy, soft in texture; dorsal blood vessel in shallow to deep groove
	- dorsal blood vessel on surface of ovary	

Table 2 . Histological criteria for classifying sex and maturity in walleye and sauger.

Maturity Category	Sex	
	Female	Male
Mature	- Residual eggs	-Dorsal blood vessel in deep groove especially posteriorly
	- spent characteristics: flaccid, sac-like appearance with wrinkles in ovarian wall	-spent characteristics: flaccid, sharply tapered, with shallow longtitudinal folds in testicular wall
Immature	- No residual eggs	-Dorsal blood vessel on surface over entire length
	- No spent characteristics	-No spent characteristics
	- Primary oocytes only	
Developing	- Eggs visible to eye	-Testes enlarged
	- no residual eggs	-Dorsal blood vessel in groove over entire length
	- no spent characteristics	-no spent characteristics
	- large proportion of later-stage oocytes	
Mature uncertain	- No residual eggs	-Dorsal blood vessel in groove
	- Definite spent characteristics	-questionable spent characteristics
	- small proportion of later-stage oocytes	
Immature uncertain	- No residual eggs	-Dorsal blood vessel in shallow groove
	- Questionable spent character-istics	-no spent characteristics
	- primary oocytes only	
Developing uncertain	- poorly developed	-poorly developed

be discerned: primary oocytes and later-stage oocytes. Phases of oocyte growth, described by Koshelev (1963) and others, could not be determined as follicular membrane structure, degree of yolk depositon or vacuolation, chromatin structure, etc. could not be distinguished.

Analyses

All years' data were pooled and broken down by season. Seasons were chosen arbitrarily as follows:

Spring: May 26 to June 30

Summer : July 1 to August 31

Fall: September 1 - October 5

Routine statistical analyses were performed according to Snedecor and Cochran (1967).

To determine the degree of error in visually classifying sex and maturity each fish was given an error score of one or zero. A zero score was assigned when the visual classification of sex and maturity was equal to the histological classification. In all other cases a score of one was assigned.

The description of the frequency of mature fish at various ages or sizes was based on a logistic model:

$$Y_x = \frac{k}{1 + e^{-b(x - x_o)}}$$

where Y_x = frequency of mature fish among all fish aged x or in length class x.

k = frequency of mature fish among the oldest age groups or largest length classes.

x_o = age or size class at inflection point.

b = slope.

It was assumed that k = 100%. To facilitate fitting a regression by least squares, the data were transformed as follows:

$$-\log_e \left(\frac{k - y}{y} + 1\right) = -bX_o + bX$$

Otolith ages were used for all age-specific analyses. Otoliths were aged according to Erickson (1979).

A 10 mm length interval was arbitrarily chosen for size-specific determinations of maturation rates.

The mean weighted age of onset of sexual maturity was calculated as follows:

$$Z = \frac{A_1 K_1 + A_2 (K_2 - K_1) + A_3 (K_3 - K_2) + \ldots + A_n (K_n - K_{n-1})}{K_1 + (K_2 - K_1) + (K_3 - K_2 + \ldots + (K_n - K_{n-1})}$$

where A = age (years)

K_n = % of mature fish in the n^{th} age class.

This is a corrected version of Abrosov's (1967) original formula.

Age-specific and size-specific maturation rates were determined for female saugers only, since sample sizes of male saugers and male and female walleyes were too small.

Summer maturation rates were not determined since maturity errors and uncertainties were highest in that season.

All-seasons maturation rates were based on mature fish from all seasons and on immature fish from spring and fall only, since female maturity errors and uncertainties were highest in summer.

In order to determine autumnal maturation rates the season was extended to include August since females showed gonadal development in that month and numbers of fish in September and October were comparatively small. Autumnal maturation rates based on visual classifications were made by equating developing fish with mature fish since very few females were classified as being mature. Data from the fall 1979 index fishing program were used to determine a maturity curve for comparative purposes. The program utilized visual classifications and scale ages to determine the age-specific frequencies of mature fish. The developing category was not used. All fish showing gonadal development were classified as being mature.

Whether maturity is size-specific or age-specific was determined for female saugers only, since sample sizes of male saugers and male and female walleyes were too small.

RESULTS

A total of 195 walleyes and 361 saugers were collected (Appendix A). Of these 44% were female saugers (Fig. 1, Appendix B).

The total degree of error in classifying maturity was highest in summer and lowest in spring (Table 3). Sexing errors were most frequent in fall. Male and female maturity errors were most frequent in summer and fall. Maturity was histologically uncertain most often in spring and summer.

A X^2 test of visual versus histological determinations of sex, irrespective of maturity, showed that significant differences did not occur (Appendix C).

An examination of the seasonal proportions of walleyes and saugers in each sex and maturity category by visual and histological classification methods (Fig. 2, Appendix D) indicates the following trends:

1. In spring and summer, a tendency to underestimate the proportions of mature individuals and to overestimate the proportions of immature individuals.
2. In summer and autumn, a tendency to overestimate the proportions of developing females.
3. In autumn, a tendency to underestimate the proportions of mature and immature females.
4. In autumn it is practically impossible to distinguish between developing and mature males by visual or histological means. Thus, no

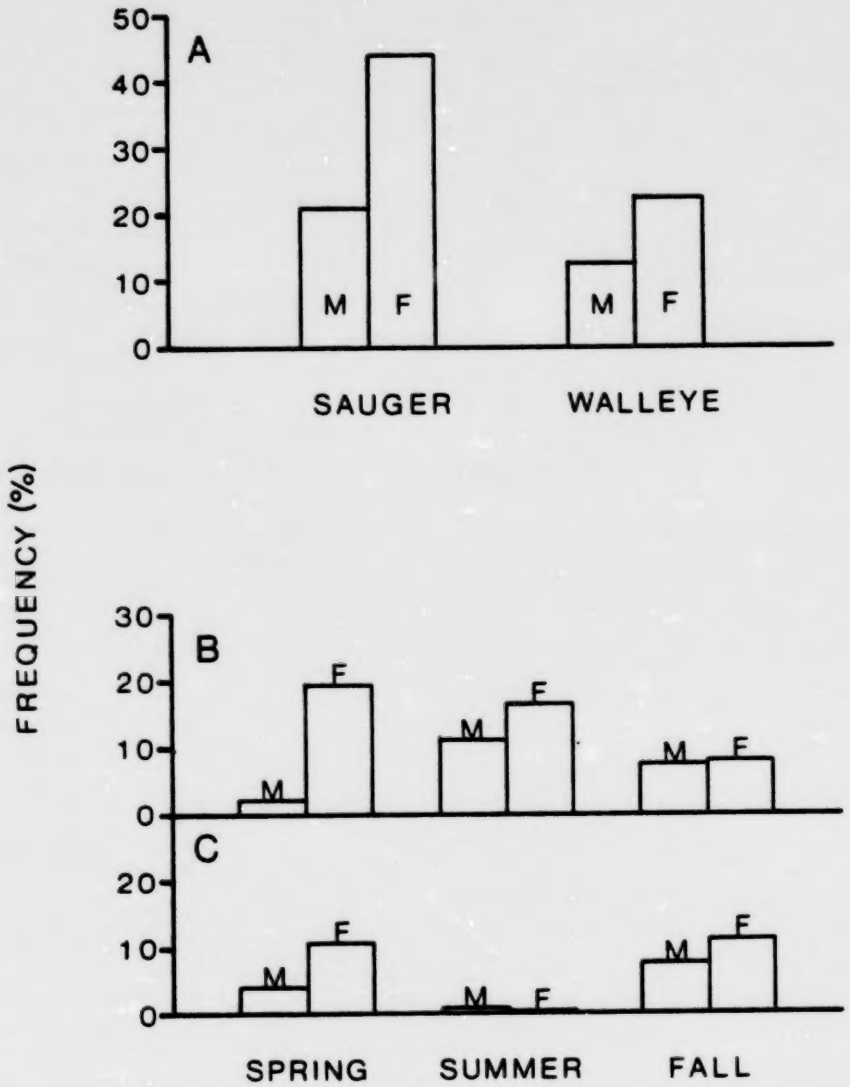

Fig. 1. Proportions of total sample comprised by gonads of each species. M = males, F = females .

A. Total proportions of saugers and walleyes from all seasons.
B. Seasonal proportions of sauger sexes.
C. Seasonal proportions of walleye sexes.

Table 3. Sauger and walleye seasonal % error scores.

Type of error	Season		
	Spring	Summer	Fall
sexing error	2.2	3.1	9.4
male maturity error	0.6	9.9	1.6
female maturity error		9.9	5.7
maturity uncertain	6.8	23.0	4.2
Totals	9.6	45.9	20.9
N	177*	161	192

*26 saugers excluded because gonads were in poor condition.

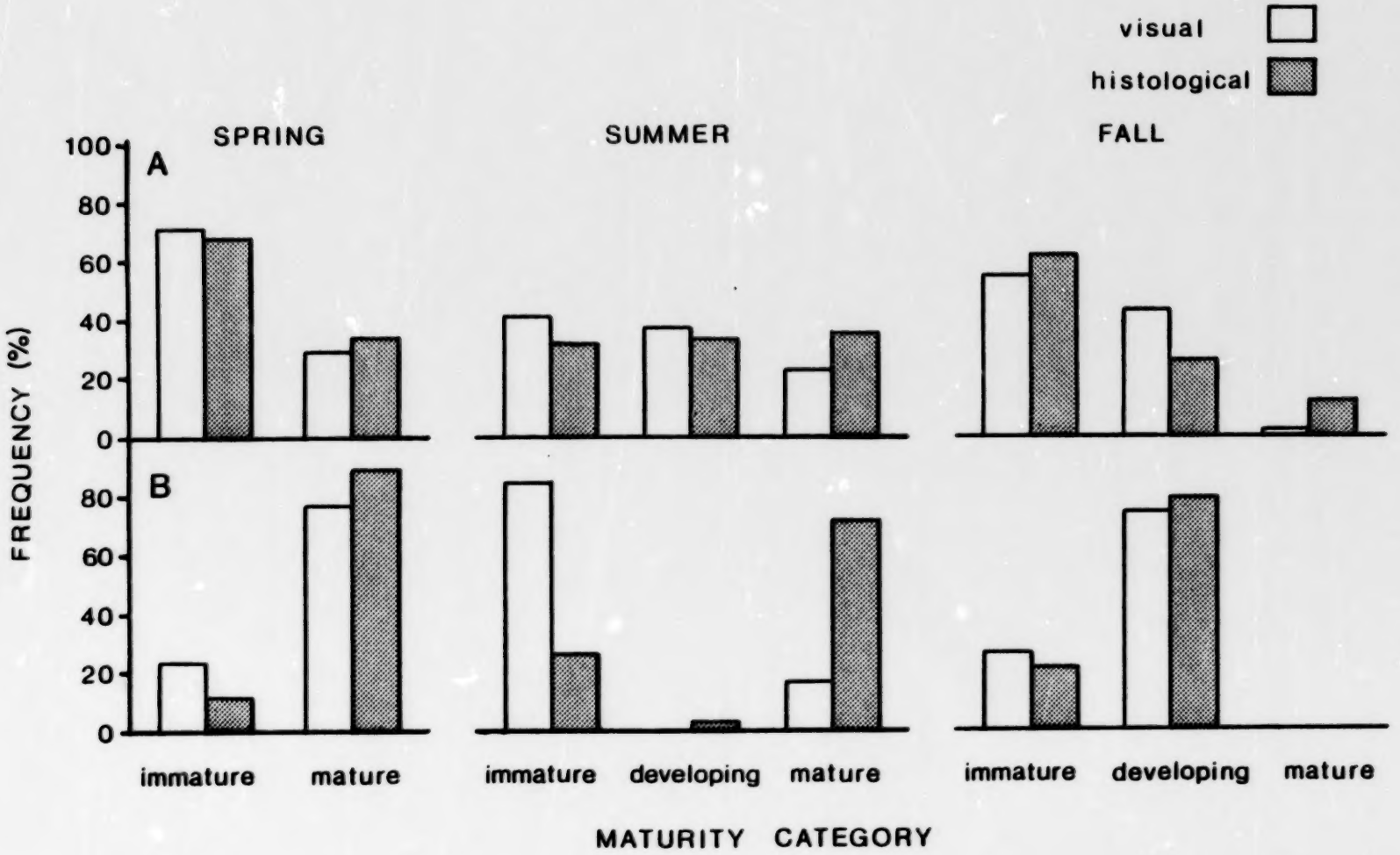

Fig. 2. Seasonal differences between visual and histological determinations of sauger and walleye states of maturity. Fish in the uncertain maturity categories are excluded. A - females, B - males.

males were classified as being mature. There was still an underestimate of the proportion of developing males. As in spring and summer, there was a tendency to overestimate the proportions of immature males.

Age-specific and size-specific seasonal maturity rates were determined from least squares regression analysis of transformed frequencies of mature fish (Tables 4, 5). Maturity rates based on visual classifications were less than those based on histological classifications (Figs. 3,4), except for all-seasons size-specific maturity rates (Fig. 4A). The greatest differences between visual and histological maturity rates occurred in fall (Figs. 3C, 4C). Slopes of histological maturity curves (Tables 6,7) were greater in spring and fall than in all-seasons. Slopes of visual maturity curves were greater in spring and lesser in fall than in all-seasons.

Least squares regression analyses of curves in figures 3 and 4 showed:

1. Non-significant relationships of frequencies of mature fish and age in spring by the histological method and in autumn by the visual method (Table 6).

Table 4. Seasonal frequencies of mature fish in each age class determined by histological and visual classification methods.

Age Class (Yrs)	Frequency (%)					
	All-Seasons		Spring only		Fall only	
	Histological	Visual	Histological	Visual	Histological	Visual
2	0				0	0
3	18.18	0	0	0	18.18	40.00
4	25.00	20.00	7.69	10.00	42.86	72.73
5	52.94	36.00	14.81	11.76	66.67	80.77
6	78.79	53.33	75.00	51.22	100.00	75.00
7	100.00	83.33	100.00	77.78		100.00
8		100.00		100.00		
N	138	142	82	101	37	87

Table 5. Seasonal frequencies of mature fish in each 10 mm length interval determined by histological and visual classification methods.

Length interval (mm)	Frequency (%)					
	All-Seasons		Spring only		Fall only	
	Histological	Visual	Histological	Visual	Histological	Visual
250-259.9						0
260-269.9						20.00
270-279.9	0	0	0	0	0	83.33
280-289.9	14.29	8.70	5.88	5.00	33.33	33.33
290-299.9	40.00	24.00	16.67	11.11	60.00	73.33
300-309.9	66.67	47.37	60.00	40.00	66.67	90.00
310-319.9	92.31	68.75	85.71	60.00	100.00	87.50
320-329.9	70.59	53.85	62.50	55.56	33.33	75.00
330-339.9	85.71	83.33	88.89	88.89	75.00	88.89
340-349.9	100.00	75.00	100.00	66.67	100.00	100.00
350-359.9		100.00		100.00		
N	138	142	82	101	37	87

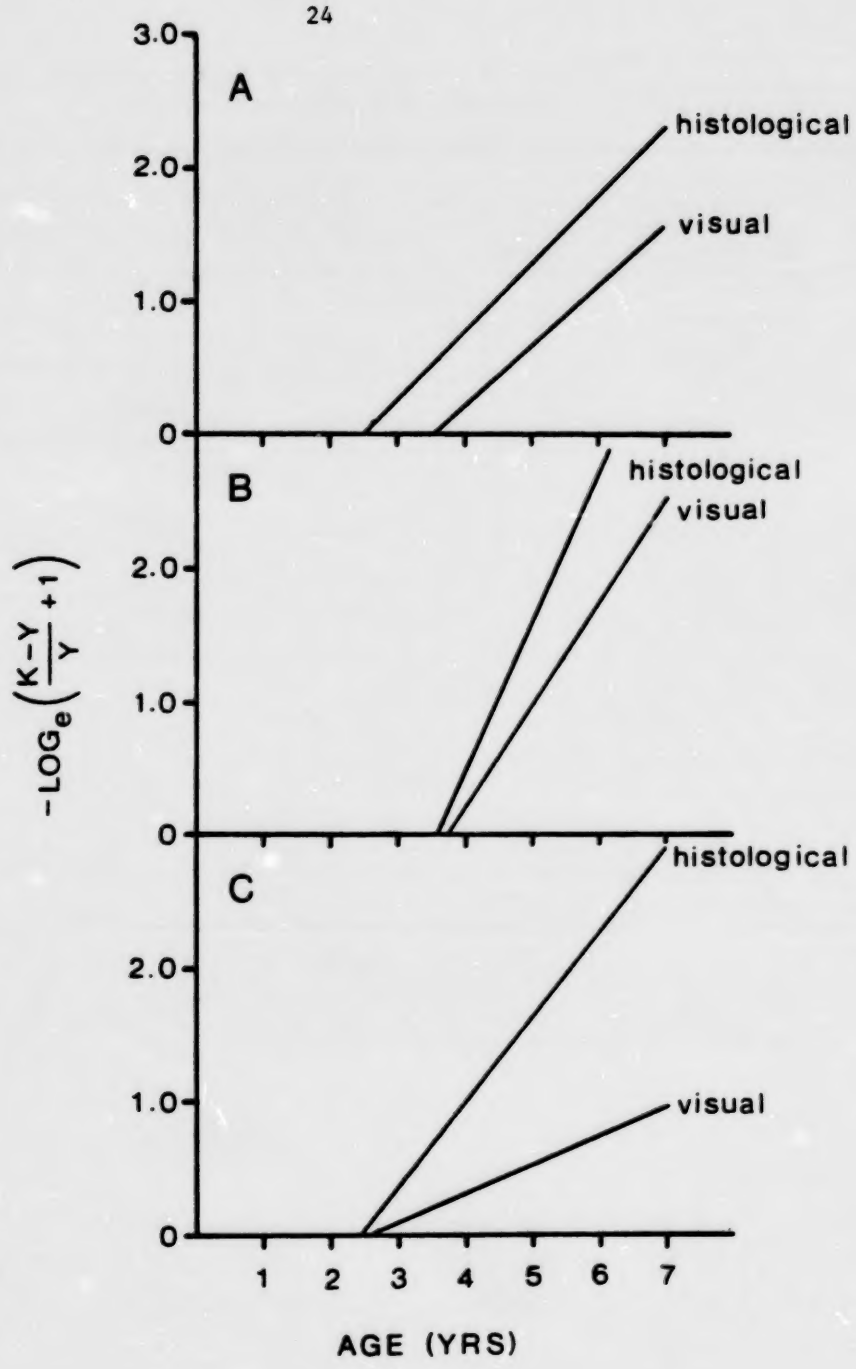

Fig. 3. Age-specific maturity curves of female saugers. A - all-seasons, B - spring, C - fall.

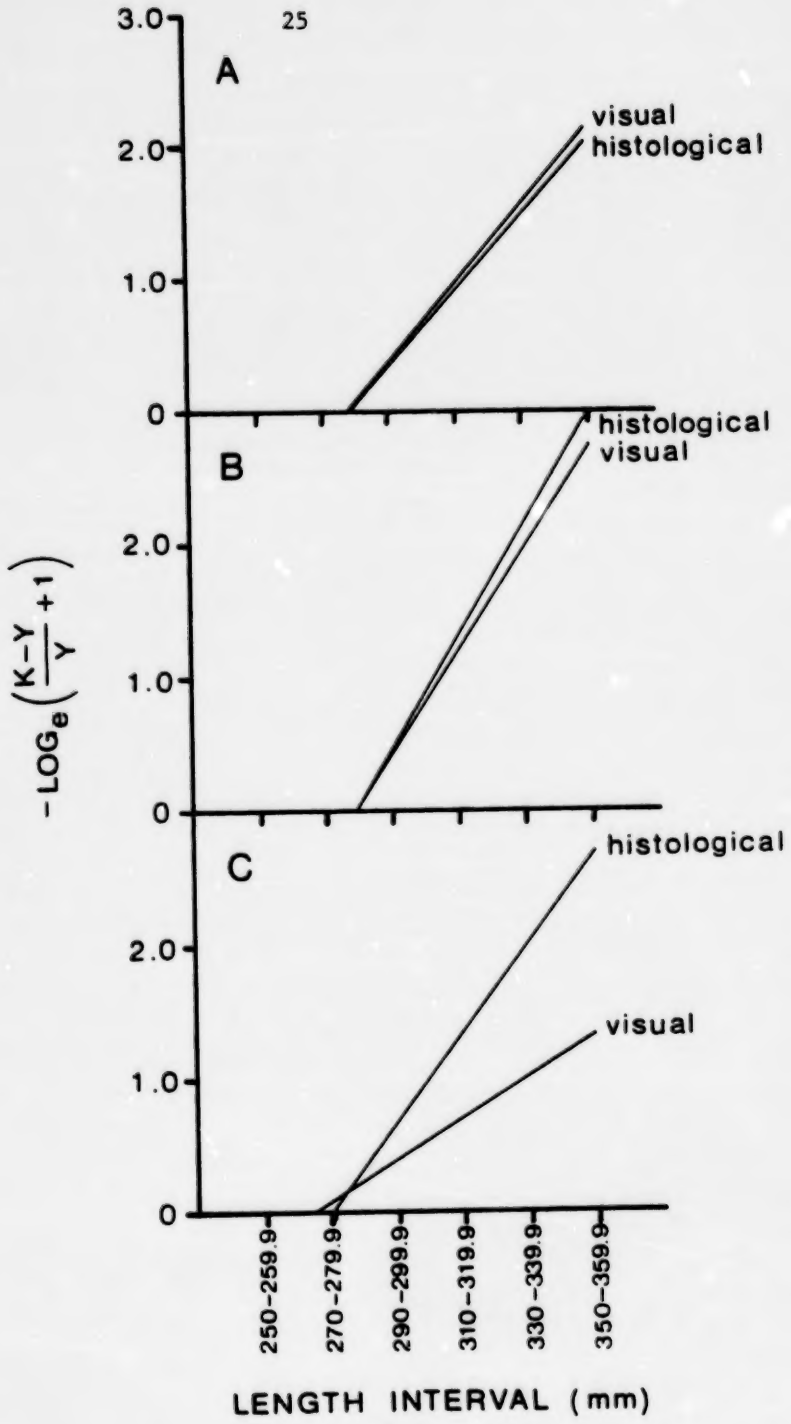

Fig. 4. Size-specific maturity curves of female saugers. A - all-seasons, B - spring, C - fall.

Table 6. Linear equations describing various age-specific maturation rates of female saugers.

Season	Type of maturity determination	Linear equation $-\log_e (\frac{k - y}{y} + 1) = -bx_o + bx$	Inflection point (yrs)	Correlation coefficient	Age of first maturity	Age at Y = 1.0	Age at Y = 0.5	Abrosov's mean weighted age of onset of sexual maturity
All-seasons	histological	Y = -3.309 + 0.515 X	6.43	0.99	3	7	5.08	5.25
	visual	Y = -3.431 + 0.467 X	7.34	1.00	4	8	5.86	6.07
Spring	histological	Y = -7.278 + 1.138 X[1]	6.40	0.97	4	7	5.79	6.53
	visual	Y = -5.535 + 0.763 X	7.26	0.95	4	8	6.35	6.49
Fall	histological	Y = -3.583 + 0.649 X	5.52	0.98	3	6	4.45	4.72
	visual	Y = -1.330 + 0.199 X[2]	6.68	0.79	3	7	3.20	6.68

[1] non-significant (F = 16.54, 1 and 2 d.f., P = 0.05)

[2] non-significant (F = 3.37, 1 and 3 d.f., P = 0.05)

Table 7. Linear equations describing various size-specific maturation rates of female saugers.

Season	Type of maturity determination	Linear equation $-\log_e (\frac{k - y}{y} + 1) = -bx_o + bx$	Inflection point (mm)	Correlation coefficient	Length interval of first maturity (mm)	Length interval at Y = 1.0 (mm)	Length at Y = 0.5 (mm)
All-seasons	histological	Y = -10.216 + 0.031 X	325.44	0.835	280 - 289.9	340 - 349.9	303.36
	visual	Y = -10.922 + 0.032 X	336.78	0.867	280 - 289.9	350 - 359.9	315.41
Spring	histological	Y = -16.579 + 0.051 X	324.15	0.873	280 - 289.9	340 - 349.9	310.60
	visual	Y = -14.677 + 0.044 X	335.23	0.883	280 - 289.9	350 - 359.9	319.39
Fall	histological	Y = -10.724 + 0.035 X^1	309.38	0.928	280 - 289.9	340 - 349.9	289.39
	visual	Y = -10.216 + 0.031 X^2	326.02	0.676	260 - 269.9	340 - 349.9	281.28

[1] non-significant (F = 6.19, 1 and 2 d.f., P = 0.05)

[2] non-significant (F = 5.06, 1 and 7 d.f., P = 0.05)

2. Non-significant relationships of frequencies of mature fish and size in autumn by histological and visual methods (Table 7).

The best estimate of age-specific and size-specific maturity rates were determined from all-seasons histological data (Figs. 5B, 6B). Comparing these curves to maturity curves obtained visually in spring and fall (Figs. 5,6), it can be seen that:

1. Visually classifying maturity in spring overestimates age-specific and size-specific maturity rates.
2. Visually classifying maturity in autumn severely underestimates the age-specific maturity rate and moderately underestimates the size-specific maturity rate.
3. There is very little difference in autumnal age-specific maturity rates determined from this study (Fig. 5C) and from the 1979 index fishing program (Fig. 5D), even though sample sizes and aging structures were different. Eighty-seven fish aged by otoliths were used in this study; 241 fish aged by scales were used in the index fishing program.

Analysis of covariance of growth curves of spring and autumn samples showed no significant difference in slopes ($F = 1.01$, 1 and 4 d.f., $P = 0.05$).

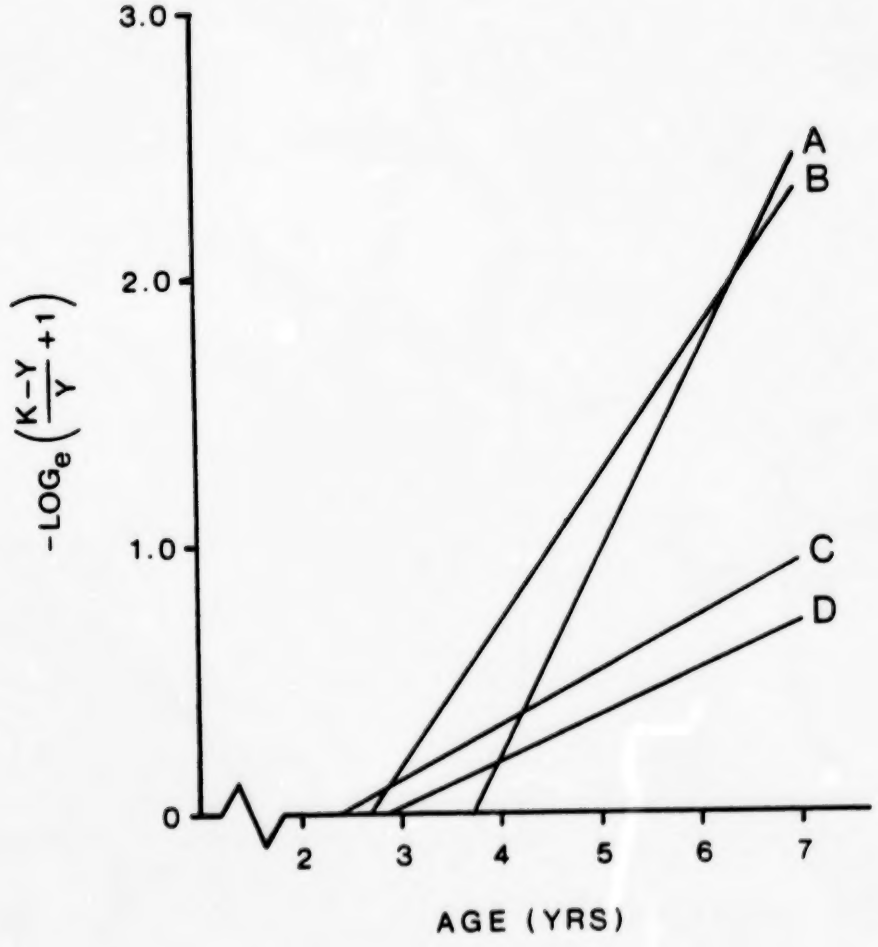

Fig. 5. Age-specific maturity curves of female saugers.
A - spring visual, B - all-seasons histological,
C - fall visual, D - index fishing visual.

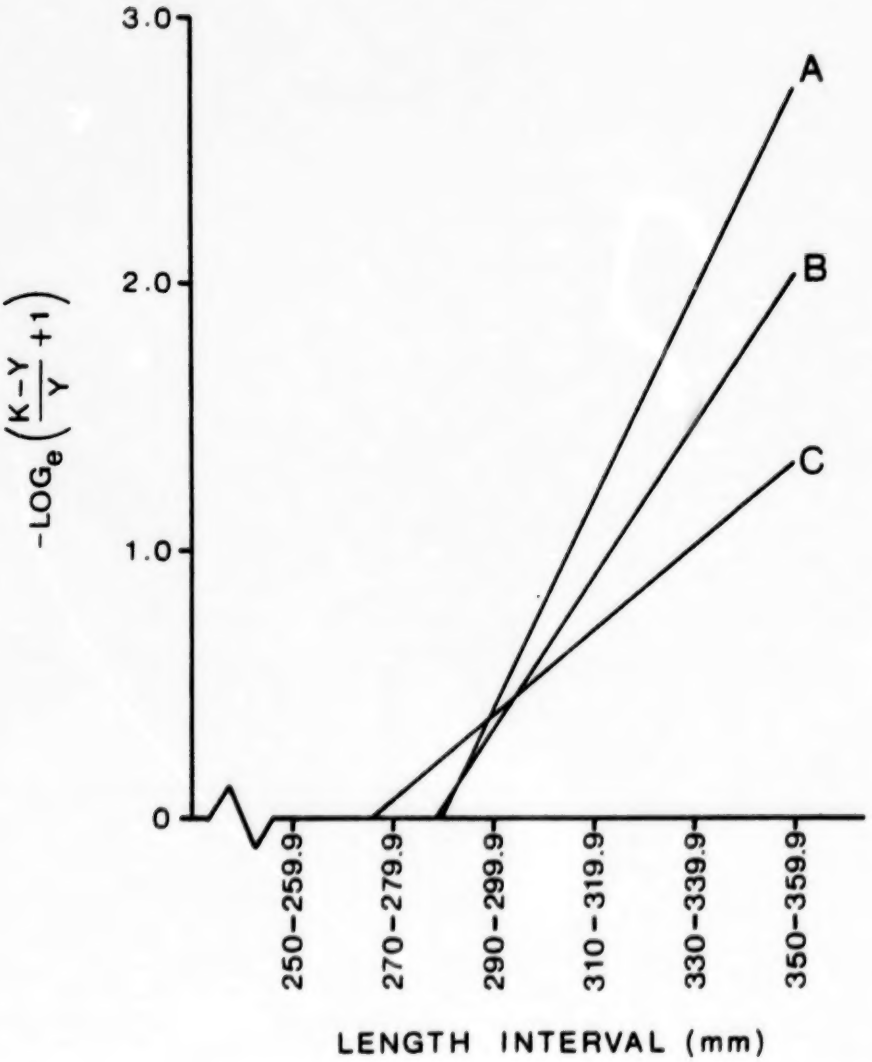

Fig. 6. Size-specific maturity curves of female saugers. A - spring visual, B - all seasons histological, C - fall visual.

The mean weighted ages of onset of sexual maturity in female saugers (Abrosov 1967) were greater than the mean ages of maturity derived from fitted maturity curves (Table 6). The greatest difference (3.48 years) between values obtained by these two methods occurred in the fall visual category. The best probable estimate of the mean age at maturity (5.08 years) was determined from the maturity curve of all-seasons histological data. This value is 1.27 years less than that derived from the spring visual curve and is 1.88 years greater than that derived from the fall visual curve.

The best probable estimate of the mean size at maturity (303.36 mm) was determined from the maturity curve of all-seasons histological data (Table 7). Visual spring and fall data yielded mean sizes at maturity greater and lesser, respectively, than all-seasons data.

At any given age the mean length of mature female saugers was greater than that of immature female saugers (Fig. 7).

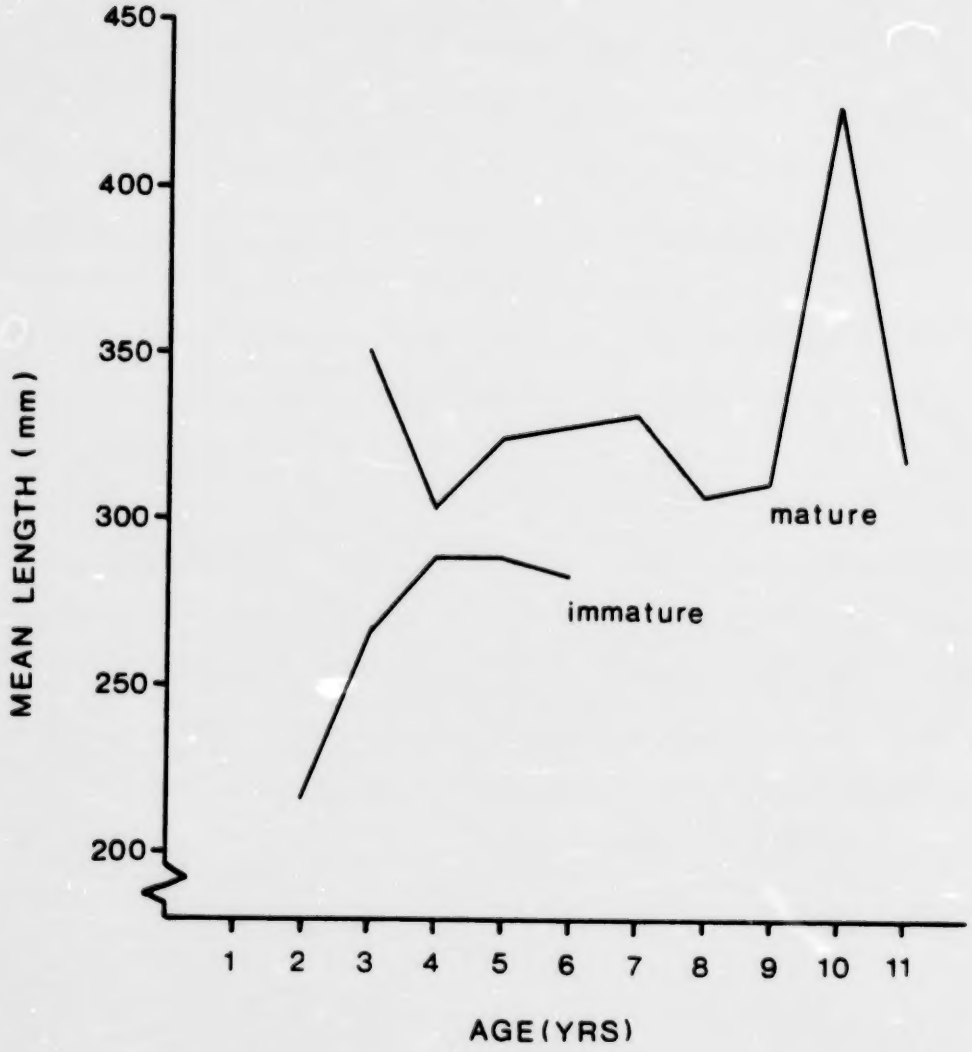

Fig. 7. Differences in age-specific mean lengths of immature and mature female saugers. N = 163. Maturity was determined histologically.

DISCUSSION

By staining ovarian tissue with aceto-carmine only primary oocytes and later-stage oocytes could be discerned. Primary oocytes were of smallest size, irregular in shape, with a nucleus occupying approximately 50% of the cell. Nuclei stained lightly and often had a pitted appearance. Primary oocytes occurred in all stages of the maturation cycle but during late summer and autumn later-stage oocytes became more frequent. These were larger, more rounded, and contained a less defined but more densely-staining nucleus.

Seasonal error scores were used in an attempt to quantify discrepancies between visual and histological maturity determinations. While the degree of uncertainty in histological determinations cannot be considered a measurement of error,it is an indication of the degree of difficulty in distinguishing between immature and mature individuals. During spring, spent characteristics were still quite obvious so that the degree of uncertainty was low. Uncertainties were much higher in summer since spent characteristics, particularly in males, became much less obvious as recovery proceeded. During late summer,an estimate of uncertainty in females was confounded by gonadal development. Uncertainties in autumn could not be reliably accounted for since both new-spawners and former-spawners showed gonadal development.

The logistic distribution of age-specific or size-specific frequencies of mature fish has been used by very few authors to describe reproductive dynamics. Wolfert (1969)

described differences between the size-specific proportions of mature female walleyes from the eastern and western basins of Lake Erie. Bell et al. (1977) used linear regressions to determine median ages of maturity of male and female whitefish from Lesser Slave Lake.

Linear regressions yield two important parameters: b, the instantaneous rate of maturity and x_o, the inflection point. It is hypothesized that the values of these parameters will increase as fishing effort increases because fish stocks respond to increases in fishing effort by maturing at faster rates. Long-term changes in the slope of maturity curves may reflect this response. The y-intercept and the age or size at which k is attained should also be considered. For example, the slopes of maturity curves may be identical for males and females of a species, but the male y-intercept and age or size at which k is attained may be less than those of females. This implies that males and females mature at the same rate but that males begin to mature before females.

The exact straight line formula of the logistic model is as follows:

$$-\log_e \left(\frac{k - y}{y}\right) = -bX_o + bX$$

Adding 1 to $\left(\frac{k - y}{y}\right)$ eliminates the infinity value produced by $\log_e \left(\frac{k - y}{y}\right)$ when Y = 0 or Y = 100. Adding 1 to $\left(\frac{k - y}{y}\right)$ also changes the position of the points with respect to the y-axis so that the mean age of maturity is always higher than it would be if 1 was not added. Y values of 0 and 100 were not included in linear transformations.

Abrosov (1967) calculated what he called the mean weighted age of onset of sexual maturity:

$$Z = \frac{A_1 K_1 + A_2 K_2 + A_3 K_3 + \ldots + A_n K_n}{K_1 + K_2 + K_3 + \ldots + K_n}$$

where $A_1, A_2, \ldots A_n$ are ages of fish taking part in spawning for the first time. $K_1, K_2, \ldots K_n$ are percentages of sexually mature fish in the n^{th} age class.

Because spawners comprising K_n include fish which have spawned previously one or more times, Abrosov states that the denominator of Z will exceed 100 and he corrects for this by:

$$Kn = 100 - (K_n - 1)$$

This same argument may be extended to all other values of K except K_1. Thus the corrected formula is:

$$Z = \frac{A_1 K_1 + A_2 (K_2 - K_1) + A_3 (K_3 - K_2) + \ldots + A_n (K_n - K_{n-1})}{K_1 + (K_2 - K_1) + (K_3 - K_2) + \ldots + (K_n - K_{n-1})}$$

The Z value is commonly equated to the age at which 50% of the individuals are mature although this assumption is not always correct. The use of a fitted maturity curve eliminates anomalies caused by negative $A_n (K_n - K_{n-1})$ values. Also, the use of fitted maturity curves in monitoring year-to-year changes in maturity rates is much more sensitive than the use of Abrosov's Z value. Z may remain relatively constant while the instantaneous maturity rate may change significantly.

The use of Abrosov's formula or of fitted maturity curves can only provide realistic estimates of maturity parameters if sample sizes are sufficiently large. In particular,the youngest age classes should be well represented since the greatest proportions of new spawners occur in these age groups. Larger sample sizes would also be required if the number of indeterminate years are many and if smaller differences in the mean age at maturity are to be detected (Appendix E).

Non-significant relationships of frequencies of mature fish and age were found in spring histological data and fall visual data. In spring, the frequency of mature 3 year-old fish was probably underestimated because 3 year-olds were not fully vulnerable to the gear. Thus too few age classes were present in the analysis. In fall, even though younger ages were well represented, the proportions of mature fish in the III and IV age classes were overestimated because new spawners were classified as being mature. Regression analysis yielded a curve with a slope not significantly different from zero.

Non-significant relationships of frequencies of mature fish and size were found for histological and visual fall data. The histological data were too few for the number of length classes used. In the visual data, proportions of mature fish in the smaller size classes were overestimated because new spawners were classified as being mature.

Maturity was shown to be size-specific. However, size-specific maturation rates are subject to an arbitrarily chosen length interval. Probit analysis would provide a more objective choice of length interval.

CONCLUSIONS

1. Specific phases of the maturation cycle cannot be determined by staining gonadal tissue with aceto-carmine. Spermatogonia cannot be resolved. By staining ovarian tissue, former spawners cannot be distinguished from new spawners because the zona pellucida cannot be resolved.
2. Seasonal discrepancies in visual determinations of maturity are smallest in spring and largest in summer.
3. In any season, visual classifications of sex, irrespective of maturity, are accurate.
4. Realistic estimates of maturity schedules can be obtained if sample sizes are sufficiently large. In particular, the youngest age classes and smallest size classes should be well represented.
5. Populations of walleyes and saugers should be sampled in spring to realistically depict maturation schedules. Sampling these species in autumn produces an underestimate of maturity rate, mean age at maturity, and mean size at maturity.
6. Maturity in female saugers is size-specific.

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LITERATURE CITED

Abrosov, V. N. 1967. Determination of commercial turnover in natural bodies of water. Problems of Ichthyology. Trans. from Russian by Am. Fish. Soc. 9: 482-489.

Bagenal, T. B., and E. Braum. 1968. Eggs and early life history, p. 159-181. In W. E. Ricker [ed.] Methods for assessment of fish production in fresh waters. Int. Biol. Programme Handb. 3; 313p.

Ball, J. N. 1960. Reproduction in female bony fishes. p. 105-135. In Symp. Zool Soc. London 1, 1960.

Balon, E. K. 1975. Terminology of intervals in fish development. J. Fish. Res. Board Can. 32: 1663-1670.

Bell, G., P. Handford, and C. Dietz. 1977. Dynamics of an exploited population of lake whitefish *Coregonus clupeaformis*. J. Fish. Res. Board Can. 34: 942-953.

Brazo, D. C., P. I. Tack, and C. R. Liston. 1975. Age, Growth, and Fecundity of Yellow Perch, *Perca flavescens*, in Lake Michigan near Ludington, Michigan. Trans. Am. Fish. Soc. 104: 726-730.

Carlander, K. D. 1945. Age, growth, sexual maturity and population fluctuations of the yellow pike-perch, *Stizostedion vitreum vitreum* (Mitchill), with reference to the commercial fisheries, Lake of the Woods, Minnesota. Trans. Am. Fish. Soc. 73: 90-107.

Deason, H. J. 1933. Preliminary report on the growth rate, dominance, and maturity of the pike-perches *Stizostedion* of Lake Erie. Trans. Am. Fish. Soc. 63: 348-360.

Derback, B. 1947. The adverse effects of cold weather upon the successful reproduction of pickerel, *Stizostedion vitreum,* at Hemming Lake, Manitoba, in 1947. Can. Fish. Cult. 2: 22-23.

Erickson, C. M. 1979. Age differences among three hard tissue structures observed in fish populations experiencing various levels of exploitation. Man. Dept. Nat. Res. Ms. Rep. 79-77, 31p.

Eschmeyer, P. H. 1950. The life history of the walleye, *Stizostedion vitreum vitreum* (Mitchill), in Michigan. Mich. Dept. Conserv. Bull Inst. Fish. Res. 3: 99p.

Forney, J. L. 1965. Factors affecting growth and maturity in a walleye population. N. Y. Fish. Gam. J. 12: 217-232.

Golovanenko, L. F. , T. F. Shuvatova, Y. P. Putina, L. S. Fedorova, and A. L. Arakelova. 1970. A physiological and biochemical description of Don pike-perch females at different stages of the sexual cycle. J. Ichthyol. Am. Fish. Soc. 10: 260-267. (Transl. from Russian).

Guerrero, R. D. III, and W. L. Shelton. 1974. An aceto-carmine squash method for sexing juvenile fishes. Progr. Fish. Cult. 36: p56.

Hoar, W. S. 1969. Reproduction, p. 1-72. In W. S. Hoar and D. J. Randall [ed.] Fish physiology, Vol. III. Academic Press, New York and London.

Hokanson, K. E. F. 1977. Temperature requirements of some percids and adaptations to the seasonal temperature cycle. J. Fish. Res. Board Can. 34: 1524-1550.

James, M. F. 1946. Histology of gonadal changes in the bluegill, *Lepomis macrochirus* Rafinesque, and the largemouth Bass, *Huro salmoides* (Lacepede). J. Morph., 79: 63-91.

Kennedy, W. A. 1949. Relationship of length, weight and sexual maturity to age in three species of Lake Manitoba fish. Bull. Fish. Res. Bd. Can. LXXX1 (1949).

Kesteven, G. L. (Ed.) 1960. Manual of field methods in fisheries biology. FAO Man. Fish. Sci. No. 1, 152p.

Koshelev, B. V. 1963. Morpho-ecological peculiarities of oogeneses in related species of percoid fishes. Tr. Inst. Morfol. Zhivotn. Acad. Nauk Severtsova 38: 189-231. (Transl.from Russian by U. S. EPA Lib. TR 77-99).

LeCren, E. D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch *(Perca fluviatilis)*. J. Anim. Ecol. 20: 201-219.

Naumov, V. M. 1956. The ovogenesis and ecology of the sexual cycle of the Murmansk herring, *Clupea harengus harengus* L. U. S. Fish and Wildlife Service, Special Scientific Report 327, p. 203-262.

Nikolsky, G. V. 1963. The ecology of fishes. Academic Press, London and New York, 352p.

Payne, N. R. 1964. The life history of the walleye, *Stizostedion vitreum vitreum* (Mitchill) in the Bay of Quinte. M. A. Thesis. Univ. Toronto, Toronto. 40p.

Priegel, G. R. 1969. Age and growth of the walleye in Lake Winnebago. Wis. Acad. Sci., Arts, Lett., 57: 121-133.

Snedecor, G. W., and W. G. Cochran. 1967. Statistical Methods. 6th Ed. Iowa State Univ. Press, Ames, Iowa. 593p.

Turner, C. L. 1919. The seasonal cycle in the spermary of the perch. J. Morph., 32: 681-711.

Wolfert, D. R. 1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. J. Fish. Res. Board Can. 26: 1877-1888.

Appendix A
Numbers of fish by date of capture

Table A1. Numbers of walleyes and saugers collected from the South Basin of Lake Winnipeg in 1976, 1977 and 1979.

Year	Date	Species	
		Walleye	Sauger
1976	May 26	59	49
	July 26		52
1977	Sept. 16	68	56
1979	June 1-15	11	55
	June 20	12	17
	July 5	5	16
	July 17		23
	Aug. 9	2	60
	Aug. 15		3
	Sept. 6	17	7
	Sept. 20	10	5
	Oct. 5	11	18
	Total	195	361

Appendix B
Seasonal proportions of sauger and walleye

Table B1. Percentage of total sample comprised by gonads of each species.

Species	Season						Total	
	Spring		Summer		Fall			
	male	female	male	female	male	female	male	female
Sauger	2.3	19.4	11.2	16.5	7.4	8.1	20.9	44.0
Walleye	4.0	10.8	0.7	0.5	7.9	11.2	12.6	22.5

Appendix C
X^2 values

Table C1. Seasonal X^2 values of visual vs histological determinations of sex of walleye and sauger irrespective of maturity.

Sex	Season								
	Spring			Summer			Fall		
	Histological	Visual	X^2	Histological	Visual	X^2	Histological	Visual	X^2
Male	35	39	0.35	66	63	0.09	85	87	0.03
Female	168	164	0.07	95	98	0.07	107	105	0.02
Totals	203	203	0.42	161	161	0.16	192	192	0.05

Appendix D
Histological and visual maturity determinations

Table D1. Differences between histological and visual determinations of sauger and walleye maturity. Percentages are in parentheses.

Species	Sex	Maturity Category*	Season							
			Spring		Summer		Fall		All Seasons	
			Histological	Visual	Histological	Visual	Histological	Visual	Histological	Visual
Sauger	Female	Immature	44(53.7)	63(62.4)	25(30.1)	37(38.9)	17(42.5)	19(40.4)	86(42.0)	119(49.0)
		Developing			28(33.7)	36(37.9)	14(35.0)	28(59.6)	42(20.5)	64(26.3)
		Mature	38(46.3)	38(37.6)	30(36.1)	22(23.2)	9(22.5)		77(37.5)	60(24.7)
		Total	82	101	83	95	40	47	205	243
	Male	Immature	3(23.1)	7(41.2)	9(25.0)	43(82.7)	2(5.3)	2(5.3)	14(16.1)	52(48.6)
		Developing			1(2.8)		36(94.7)	36(94.7)	37(42.5)	36(33.6)
		Mature	10(76.9)	10(58.8)	26(72.2)	9(17.3)			36(41.4)	19(17.8)
		Total	13	17	36	52	38	38	87	107
Walleye	Female	Immature	43(86.0)	48(87.3)	2(100.0)	3(100.0)	38(77.6)	38(66.7)	83(82.2)	89(77.4)
		Developing					9(18.4)	17(29.8)	9(8.9)	17(14.8)
		Mature	7(14.0)	7(12.7)			2(4.1)	2(3.5)	9(8.9)	9(7.8)
		Total	50	55	2	3	49	57	101	115
	Male	Immature	1(4.5)	2(9.1)	1(33.3)	4(100.0)	15(34.1)	20(42.6)	17(24.6)	26(35.6)
		Developing					29(65.9)	27(57.4)	29(42.0)	27(37.0)
		Mature	21(95.5)	20(90.9)	2(66.7)				23(33.3)	20(27.4)
		Total	22	22	3	4	44	47	69	73

*Fish in the uncertain maturity categories are excluded.

Appendix E
Minimum sample sizes

Table E1. Minimum age-specific sample sizes*.

Number of indeterminate years	Significant difference between mean age at maturity (yrs.)			
	0.25	0.5	0.75	1.0
3	96	24	11	6
4	288	72	32	18
5	640	160	71	40

* based on the following formula given by Lysack (pers. comm.):

$$n = \frac{a^2 (0.5\ b)}{c^2}$$

where n = minimum sample size.

a = degrees of freedom.

b = number of indeterminate years (number of age classes where $Y \neq 0$ or 100).

c = significant difference between mean age at maturity in years.